Perameles bowensis, a New Species of *Perameles* (Peramelemorphia, Marsupialia) from Pliocene Faunas of Bow and Wellington Caves, New South Wales

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Muirhead, J., Dawson, L., and Archer, M. (1997). *Perameles bowensis*, a new species of *Perameles* (Peramelemorphia, Marsupialia) from Pliocene faunas of Bow and Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 163-174

Perameles bowensis n. sp. is described from the early Pliocene Bow Local Fauna and is phylogenetically compared to other species of *Perameles*. This species is the second species of Tertiary *Perameles*. It appears to be closer to Recent species of *Perameles* than to the early Pliocene *Perameles allinghamensis*. Specimens from Pliocene sediments of Wellington Caves are also considered to represent *P. bowensis*. The presence of this species in both the Bow and Big Sink Local Fauna (Wellington) provides further support to the correlation of these faunas.

Manuscript received 17 June 1996, accepted for publication 23 October 1996.

KEYWORDS: Bandicoot, *Perameles*, Pliocene, Wellington Caves, Bow Local Fauna, Big Sink Local Fauna

INTRODUCTION

Perameles allinghamensis Archer, 1976 was the first species described from the fossil record of the otherwise modern genus *Perameles*. It was recovered from the early Pliocene Bluff Downs Local Fauna in north Queensland (Archer 1976). Other Tertiary occurrences of *Perameles* have been reported, e.g. the Miocene Tarkarooloo and Kutjamarpu Local Faunas (Rich et al. 1982), however, none of these have been formally described and re-examination of this material indicates that these specimens have been incorrectly attributed to *Perameles* (Rich et al. 1991). *Perameles bowensis* from the Bow Local Fauna of northern New South Wales is the second species of Tertiary *Perameles* described.

There are currently five recognised species of *Perameles*. These are *P. nasuta* Geoffroy, 1804, *P. gunnii* Gray, 1838, *P. bougainville* Quoy and Gaimard, 1824, *P. eremiana* Spencer, 1897 and the Pliocene *P. allinghamensis* Archer, 1976. While Tate (1948) regards *P. bougainville*, *P. eremiana*, *P. fasciata* and *P. notina* to be possible local races of a widespread southern species, Marlow (1962) considers all of these to be distinct species. Here these forms are collectively regarded as *P. bougainville* except for *P. eremiana* which is considered distinct following Mahoney and Ride (1988) and Seebeck et al. (1990). All comparative specimens used in this work representing *P. bougainville* were collected as subfossil specimens from the Nullarbor Plains in Western Australia and therefore do not necessarily represent all possible races and variants of this species.

Dental nomenclature used follows that of Flower (1864) and Luckett (1993) where the adult (unreduced) tooth formula of marsupials is P1-3 and M1-4. Tooth morphology nomenclature follows Muirhead (1994). Classification follows Aplin and Archer (1987). Catalogue number abbreviations are AMF; Australian Museum palaeontological collection.

Figure 1. *Perameles bowensis* type material. A and A' = AMF98810 stereo occlusal views. B and B' = AMF98809 stereo occlusal views. C and C' = AMF98811 stereo occlusal views. D = AMF98811 lateral view of lingual side. Scale bar at A = 1mm. Scale bar at B = 2mm. Scale bar at C and D = 1mm.

SYSTEMATICS

Supercohort: Marsupialia (Illiger, 1811) Cuvier, 1817
Cohort: Australidelphia Szalay, 1982
Order: Peramelemorphia (Kirsch, 1968) Aplin and Archer, 1987
Family: Peramelidae (Gray, 1825), (sens. Groves and Flannery,1990)
Perameles bowensis n. sp.

Holotype

AMF98809 (Fig. 1B) Right M^3

Paratypes

AMF98810 (Fig. 1A) RM^2; AMF98811 (Fig. 1C and D) RP^3; AMF98812 (Fig. 2C and D) RM_3; AMF98813 (Fig. 2A and B) LM_1.

Specific etymology

The species name is in reference to the type locality.

Type locality and age

The Bow Local Fauna lies within unnamed roadcut sediments in northeastern New South Wales. This fauna has been dated at early Pliocene based on biocorrelation with the radiometrically dated Bluff Downs Local Fauna (Skilbeck 1980, Flannery and Archer 1984, Rich et al. 1991).

Diagnosis

Perameles bowensis differs from all other species of *Perameles* in the following combination of features: 1) small size, 2) greater development of metastylar region on M^3, 3) shallow ectoflexus on M^3 and none on M^2, 4) small hypocone on M^3, 5) large lingual displacement of stylar cusps on M^2, 6) small development of parastylar region on M^2, 7) strongly curved preparacrista on M^2, 8) anterobuccal cingulum on M^3 and M^2 but not connecting to preprotocrista, 9) P^3 ovoid in shape with well developed posterior heel not continuing anteriorly beyond lingual side of primary cusp, 10) no anterior cusp on P^3, and 11) posthypocristid on M_1 not continuous to posterolingual corner of crown.

Perameles bowensis is phenetically most similar to *P. eremiana* in terms of size and general shape of the molars. It differs from *P. eremiana* in the following features: 1) more continuously thick cingulum between lingual to posterior corners of P^3, 2) less well developed and shallow trough between St B and St D and associated crests on M^2 3) larger M^3 formed by the wider stylar shelf region and larger metastylar corner, 4) stylar cusps larger and wider on M^3, 5) postmetacrista entirely straight and not curved posterobuccally, 6) hypocone much smaller, 7) angle of posthypocristid orientated more oblique to the tooth length and not perpendicular, and 8) paracristid and metacristid of M_1 and M_3 are more distant.

Description

P^3 crown is short and ovoid in occlusal shape. The posterior dimension of the crown is wider than the anterior. The primary cusp is anteriorly positioned. One major crest extends posteriorly from the primary cusp to a small posterior cusp. Expansion of the crown is present as a heel from the lingual side of the primary cusp to a posterior cusp. Slight development of a heel is also present on the buccal side of the crest.

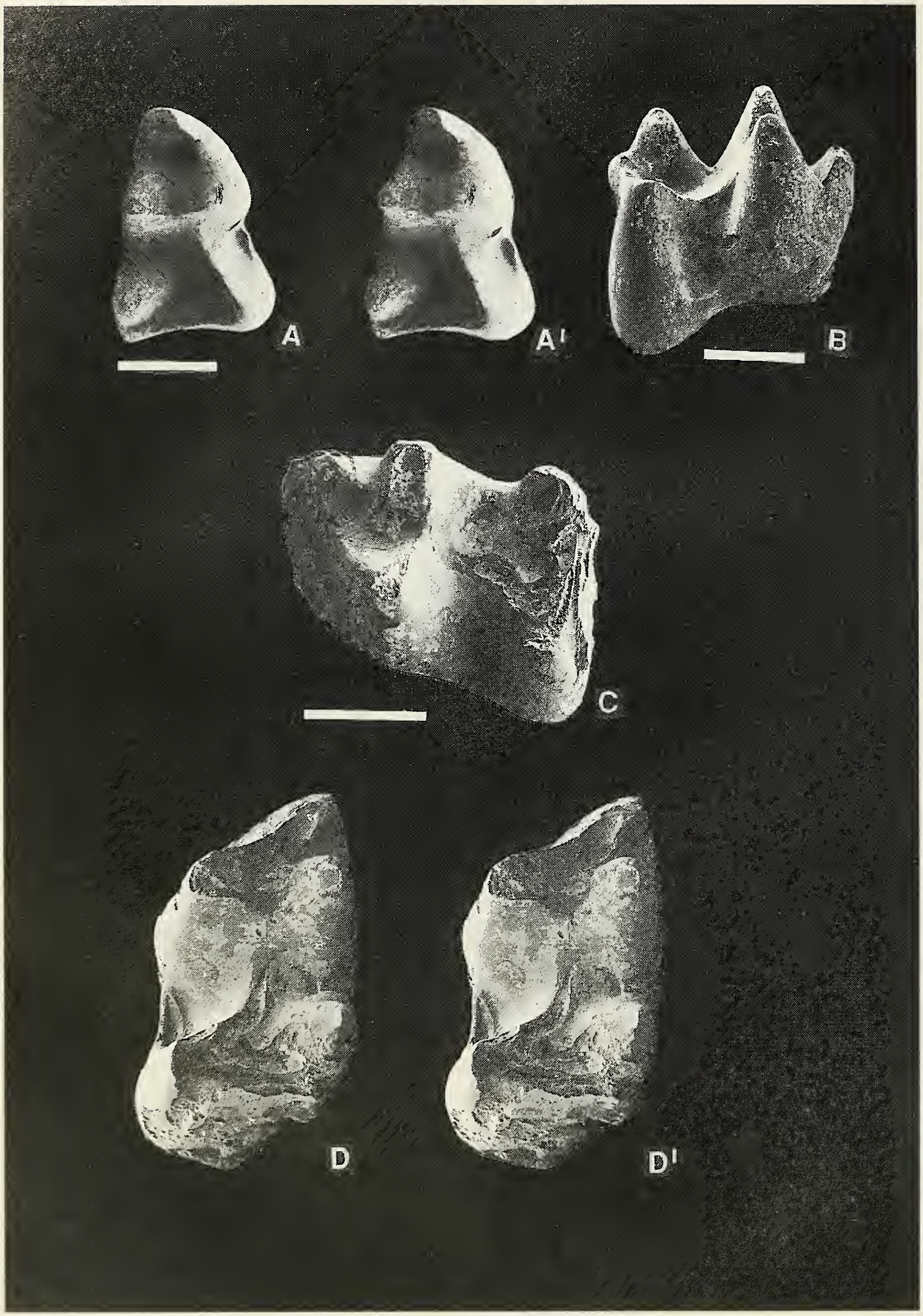

Figure 2. *Perameles bowensis* paratype material. A and A'–AMF98813 stereo occlusal views. B = AMF98813 lateral view. C = AMF98812 lateral view. D = AMF98812 stereo occlusal views. All scale bars = 1mm. C and D to same scale.

M^2 crown is roughly square in occlusal outline. The posterobuccal corner is broken. The anterior cingulum terminates below the midpoint of the preparacrista. No contact exists between the anterior cingulum and the preprotocrista. The preprotocrista terminates at the anterolingual corner of the paracone base. The crown is worn. The largest cusp is St D, followed (in decreasing height) by St B, metacone, anterior cingulum tip, paracone, protocone and hypocone. The preparacrista is short and curves to connect to the anterior cingulum tip without connection to St B. The postparacrista is slightly shorter in length, terminating around the posterior base of St B. The premetacrista is slightly longer than the preparacrista and parallel to this crest, terminating at the anterolingual base of St D. The postmetacrista is very worn and broken posterobuccally. A slight inflection exists between the protocone and hypocone. The posthypocristid terminates at the posterior base of the metacone. St B and D are the only stylar cusps present. These have strong lingual curvature. The paracone is located midway between the buccal and lingual sides of the crown. The metacone is positioned at a more lingual position. The protocone and hypocone are equidistant from the buccal edge.

M^3 crown is triangular in occlusal view. The buccal surface is the shortest of the three crown dimensions. All cusps and crests are worn. Morphology follows that of M^2 except as follows. Ectoflexus is stronger on the buccal side. The posterobuccal corner of the crown is prominently extended. St B and D do not curve lingually as much as on M^2. The anterior cingulum is shorter. The position of the paracone is more lingual and lies directly anterior to the metacone. The paracristae are longer. The postparacrista connects directly to St B rather than to the base of this cusp. The trough between St B and D is deeper at the shelf. The hypocone is small. The crest from the hypocone terminates at the lingual base of the metacone. The parastylar region is developed to a greater degree, with a larger distance between St B and the anterior cingulum tip.

The protoconid and metaconid of M_1 are approximately equal in height, followed (in decreasing height) by the entoconid, hypoconid, hypoconulid and paraconid. Of the primary cusps, the metaconid and protoconid are closer to each other than either is to the paraconid. The metaconid is directly posterior to the paraconid. The entoconid lies directly posterior to the metaconid and not connected by a preentocristid. The entoconid is conical in shape. The hypoconid is positioned almost twice as far buccally as is the protoconid. The posthypocristid is the longest crest on the crown connecting to the hypoconulid at the posterobuccal base of the entoconid. The cristid obliqua is curved, terminating at the posterior base of the protoconid and buccal to the valley in the metacristid. The entoconid lies directly lingual to the hypoconid. No anterior or posterior cingulum is present.

Morphology of M_3 follows that of M_1 except as follows. The metaconid is higher than the protoconid. The anterior cingulum is wide and without a notch, terminating at the anterior base of the protoconid. The metaconid is closer to the paraconid than to the protoconid. The protoconid is higher than the hypoconid. The protoconid is almost buccally level with the hypoconid. The cristid obliqua terminates at the base of the valley in the metacristid. No hypoconulid is present. The posthypocristid terminates at the base of the entoconid. A wear facet along the crest of the entoconid lies oblique to the anteroposterior length of the tooth.

Measurements of *P. bowensis* type material are found in Table 1.

PERAMELES BOWENSIS FROM WELLINGTON CAVES

Material collected from the Phosphate Mine Beds of Wellington Caves (NSW) during excavations by A. Osborne, M. Archer and L. Dawson in 1982–1983, has produced two bandicoot taxa (Dawson and Augee this volume). Five of these specimens appear to be *Perameles bowensis*.

All five specimens are isolated molars. Three specimens are from the Big Sink Unit and include two broken M^3s (AM F69887 [formerly WC1678], Fig 3B and AM F69899, Fig 3A) and an RM_1 (AM F69804 [formerly WC1677], Fig 3C). The remaing two specimens, a broken RM^1 (AM F69897, Fig 3E) and a RM^2 (AM F69896, Fig 3D), were retrieved from the lower 'Graded-Bedded Unit' (Osborne 1982).

The 'Graded-Bedded Unit' is separated from the Big Sink Unit by the disconformably overlying 'Conglomerate Unit' (Osborne 1983). The unconformity separating the Big Sink Unit from the overlying Mitchell Cave Beds has been estimated by Osborne (1983) to be at least late Pliocene in age. Teeth from both of these deposits appear to represent the same taxon.

TABLE 1

Measurements of specimens of *Perameles bowensis* from the Bow Local Fauna and Wellington Caves. All measurements are maximum distances in mm. Width is lingual-buccal distance on crown. Length is antero-posterior distance. Para = paracone, meta = metacone, proto = protocone, ento = entoconid, hypo = hypoconid, metad = metaconid, parad = paraconid, protod = protoconid, – = information missing or not appropriate.

Specimens from Bow

Uppers

AMF number	width	length	para-meta	meta-proto	proto-para
98810	2.54	2.50	1.27	1.18	0.77
98809	2.76	3.14	1.53	1.74	0.77
98811	1.69	1.88	–	–	–

Lowers

AMF number	width	length	ento-meta	meta-hypo	metad-parad	parad-protod	protod-metad
98813	1.61	2.52	0.92	1.12	1.02	1.07	0.69
98812	1.84	2.81	1.14	1.42	0.71	1.27	1.16

Specimens from Wellington Caves

Uppers

AMF number	width	length	para-meta	meta-proto	proto-para
69896	2.83	2.61	1.63	1.79	0.95
69899	–	3.17	1.59	–	–
69887	–	–	–	–	–
69897	–	3.34	1.78	–	–

Lowers

AMF number	width	length	ento-meta	meta-hypo	metad-parad	parad-protod	protod-metad
69804	1.63	–	1.01	1.30	–	-	0.79

These bandicoots specimens from Wellington Caves are clearly a *Perameles* rather than an *Isoodon* due to the lack of complete anterior and posterior cingulum on the upper molars (particularly the posterior molars). These specimens are within the size range of *P. bougainville* and *P. eremiana*; however they differ in morphology from these species. The only remaining species of *Perameles* of this size range is *P. bowensis* from the Bow Local Fauna.

No M^1s are available in the Bow Local Fauna attributed to *P. bowensis*. This there-

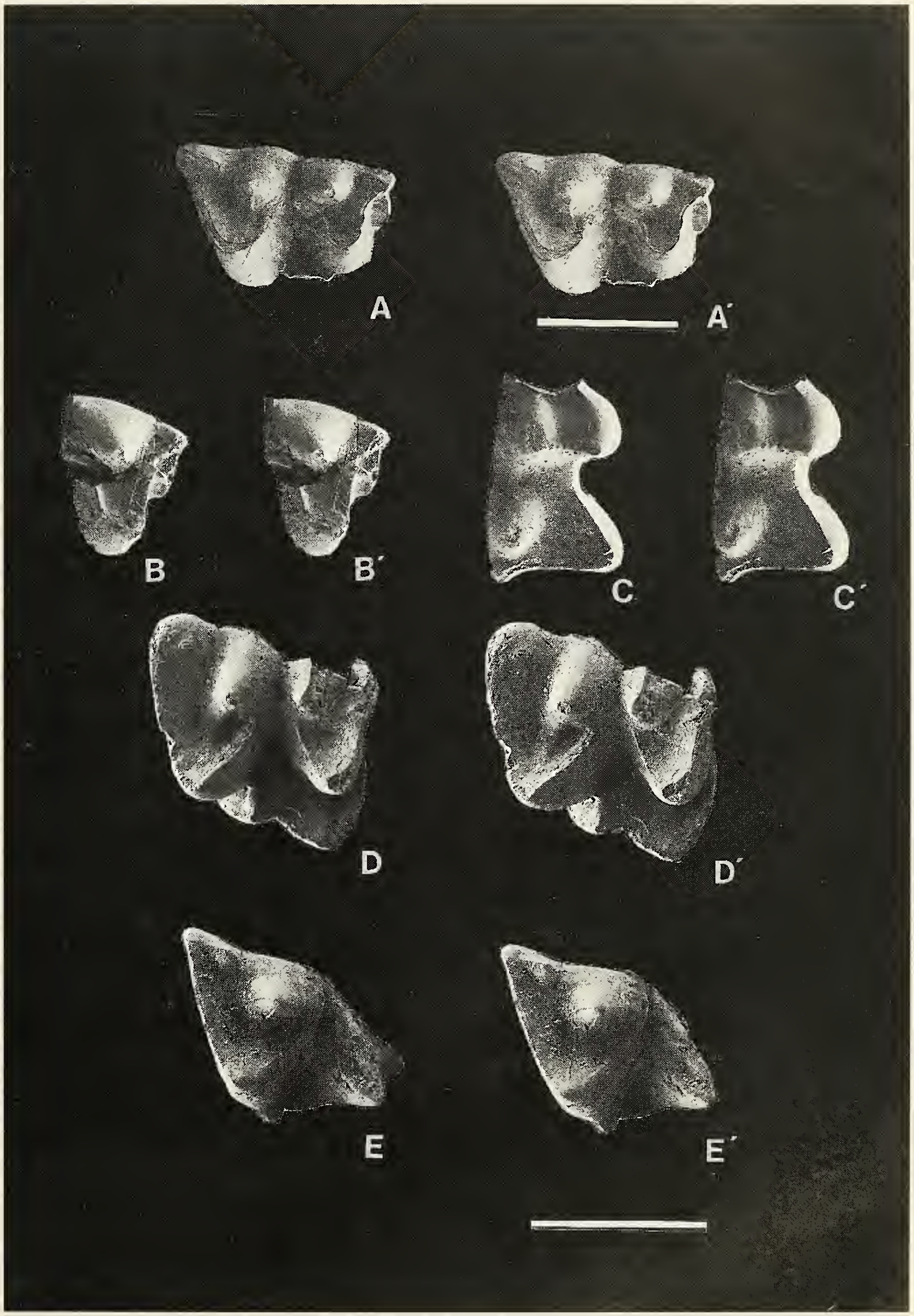

Figure 3. *Perameles bowensis* from Wellington Caves. Stereo occlusal views of specimens. A and A' = AMF69899. B and B' = AMF69887. C and C' = AMF67804. D and D' = AMF69896. E and E' = AMF69897. Scale bars = 2mm. Lower scale bar refers to all specimens except A.

fore prevents direct comparison between the M^1 from Wellington Caves and this species. The morphology of the broken M^1, however, is within the range exhibited by other species of *Perameles* and within that expected following the morphological trends of the more posterior molars of this species.

The M^2 from Wellington Caves is very similar to the corresponding tooth from *P. bowensis* in having no ectoflexus, no anterior cingulum, the same development of the posterior cingulum, the same degree of lingual displacement of the stylar cusps and a similar height of all of the cusps on the tooth. The metastylar region cannot be compared because this area has been broken in the Bow sample. The Wellington M^2 differs from the corresponding tooth from Bow in having a less concave preparacrista and greater dissimilarity in size between the protocone and hypocone. This difference in morphology between the M^2 from these sites is easily attributed to wear. The M^2 from Bow shows greater wear at the back of the lingual tip of the protocone. These is little reason to doubt the inclusion of this tooth within the morphological and size range expected for *P. bowensis*.

The M^3s from Wellington Caves are represented by two broken fragments. The larger of these includes the paracone, metacone and the stylar region of this tooth. The smaller fragment represents the paracone and parastylar region and in all respects duplicates the morphology and size shown by the more completely preserved specimen. The M^3s from Wellington are similar to the corresponding tooth of *P. bowensis* in all respects except for the lesser ectoflexus with less extension of the postmetacrista and the greater size of the St E. The size difference of St E may be attributed to wear. The extent of morphological variation for this species is unknown because of the very limited number of samples, but this degree of dfference is unlikely to be beyond that exhibited within a species.

The RM_1 differs from that of *P. bowensis* from the Bow Local Fauna only by a slightly smaller hypoconid.

There is little to preclude specimens from the Big Sink Unit and the ‘Graded Bedded Unit’ of Wellington Caves from being considered representative of *P. bowensis*. All differences between specimens may be attributed to wear or intraspecific variation. Because specimens from the type locality do not include an example of the M^1, this tooth of *P. bowensis* is described from Wellington Caves.

Description of M^1

The buccal portion of the M^1 is the only part preserved. The highest cusp on the crown is the metacone, followed (in decreasing height) by the St D, St E, paracone and St B. The parastylar region includes a small, unnotched tip on the anterobuccal corner of the crown. The paracrista does not connect to the parastylar tip but instead runs posterobuccally from the paracone to connect with St B. The postparacrista runs parallel to the preparacrista from the paracone to connect at the posterior flank of the St B. There is no ectoflexus on the crown and the buccal face of the tooth is slightly rounded. The trough between St B and St D is shallow. St D is conical in shape and there is no connection by way of a crest to the St B. The premetacrista is straight and terminates at the anterior base of St D. The postmetacrista is the longest crest on the tooth, terminating at the posterobuccal metastylar tip of the crown. It is slightly convex around the metastylar region. St E lies on the posterobuccal region of the stylar shelf. It has a short anterior and posterior crest connecting to the St D and metastylar tip respectively. The broken region at the base of the metastylar portion of the tooth indicates a triangular shape of the complete tooth with the presence of a hypocone. The posterior cingulum would, if present, not have connected to the base of the metastylar corner of the crown.

PHYLOGENETIC DISCUSSION

Aplin and Archer (1985) recognise the presence of both *Isoodon* and *Perameles* within the Bow Local Fauna. Part of the material described here as *Perameles bowensis* was that referred to as *Isoodon* (Aplin and Archer 1986, Archer 1984, Rich et al. 1991). There is no material from Bow that shares apomorphies with *Isoodon* that are not also shared with *Perameles* (e.g. enlargement of the hypocone on M^2). Apomorphies that distinguish *Isoodon* from *Perameles* are not apparent in this material such as the complete (or almost complete) and well developed anterior and posterior cingula on M^2 and M^3, and enlarged roots with a lack of distinction between root and crown. These specimens are therefore precluded from *Isoodon*. The specimens previously considered to represent *Isoodon* are now included with material referred to as *Perameles* and described here as the one species, *P. bowensis*.

Material refered to here as *Perameles bowensis* shares no apomorphies with any other genus not also shared with other species of *Perameles*. Features that *P. bowensis* has in common with other genera that are not also shared with other species of *Perameles* are symplesiomorphies. The morphology of *P. bowensis* appears to fall well within the range of diversity exhibited by modern species of *Perameles* and is therefore placed within this genus.

In general, *P. bowensis* appears to be slightly more plesiomorphic in most regards than modern species of *Perameles* but is likely to be closer to these than to *P. allinghamensis*. Of the modern species, *P. bougainville* is considered to show more plesiomorphic features of the dentition (but not cranial characters). *Perameles bougainville*, unlike *P. eremiana*, *P. nasuta* and *P. gunnii*, retains the plesiomorphic characteristics of less caniniform I^5, more linear P^3, smaller hypocones, less developed posterior cingulum, less elongated snout, retention of the hypoconulid on M_2, more equidistant paraconids, metaconids, and protoconids and an incomplete anterior cingulum on M_1.

Perameles bowensis is more plesiomorphic than all Recent species in having a smaller hypocone on the M^3, more equidistant paraconids, metaconids and protoconids on M_{1-3} with the paraconid and metaconid wider apart on M_1 than on Recent species. Of the Recent species, *P. bowensis* is phenetically similar to *P. eremiana* in having similar sized P^3 and molars except for the M^3, which is slightly larger in *P. bowensis*. The morphology of the P^3 and M^2 does not differ between these two species except that the metastylar region is smaller in *P. bowensis* and in this feature is more similar to *P. bougainville*. The lower molars of *P. eremiana* are more apomorphic in their concave cristid obliquas producing a narrower talonid. *Perameles eremiana* is also more apomorphic than *P. bowensis* in the overall smaller width of the trigonid basin produced by reduction of the distance between the paraconid and metaconid and orientation of associated crests more perpendicularly to the long axis of the tooth row. *Perameles bowensis* is plesiomorphic in this regard in having a wider trigonid which is also wider than in any other Recent species. *Perameles bowensis* is also more plesiomorphic than *P. eremiana* in having a smaller hypocone on the M^3, a feature in which it is also more plesiomorphic than all Recent species of *Perameles*.

Comparison to *P. eremiana* is restricted due to the few available samples of this species and therefore intraspecific variation for *P. eremiana* cannot be adequately assessed. However, variation to the degree needed to include *P. bowensis* into this species is much wider than that known for any other species. No species is known to vary the orientation of crests of the molars to such a degree. The variation between samples of *P. eremiana* and *P. bowensis* is therefore considered to be outside of that for a single species, and *P. bowensis* is therefore separated from *P. eremiana*. The kind of variation between these two species in some characters (e.g. crest orientation, basin width) represents the two extremes shown within the entire genus.

Perameles bowensis retains some of the plesiomorphies seen in *P. bougainville*. These are the small hypocone on M^3 and roughly equidistant paraconid, metaconid, and protoconids. The P^3 is more apomorphic than that of *P. bougainville*, with posterior thickening and a posterior heel. The poor trough development between the stylar cusps on the M^2 and the buccal termination of the cristid obliqua on the lowers are plesiomorphic features lost by all modern species.

Perameles bowensis is more apomorphic than *P. allinghamensis*. This Pliocene species is represented only by a broken isolated upper molar. The arrangement of the preparacrista and parastylar corner of the crown is entirely different to that of other species of *Perameles*. In all other species of *Perameles*, the preparacrista on the M^2 and M^3 continue past the stylar cusps to terminate at the parastylar corner. This region is of equal height or even higher than the stylar shelf and functions as an akis (a pointed cusp at the terminal end of a sharp-edged blade, [Every 1975]). This region extends anteriorly past the remainder of the crown and overlaps the proceeding molar. No anterior cingulum is present on the anterobuccal side of the tooth. The morphology of this region on *P. allinghamensis* is considered to be plesiomorphic because it is similar to that seen in dasyurids and relatively plesiomorphic bandicoots. Here the preparacrista terminates at the parastylar corner, but in addition the buccal portion of the anterior cingulum is low lying and anterior to the parastylar corner of the crown. The preparacrista bends anteriorly at this corner in other species of *Perameles*, while in *P. bowensis* the preparacrista is straight so that these regions remain separate on two levels. Further finds from the Allingham Formation representing *P. allinghamensis* may realise the possibility suggested by Archer (1976) that it represents a new genus of bandicoot.

The presence of *P. allinghamensis* in the early Pliocene Allingham Local Fauna (Archer 1976) is the earliest formally described member of this genus. Reports of the presence of *Perameles* from the Tarkarooloo and Kutjamarpu Local Faunas of the middle Miocene (Rich et al. 1982) are unsupported by more recent review (Rich et al. 1991) where these specimens have been re-classified as “Perameloidea” and appear to represent other taxa. *Perameles* sp. is also reported to be present in the Pliocene Dog Rocks Local Fauna together with *Isoodon* sp. (Whitelaw 1989, Rich et al. 1991).

Perameles bowensis is phylogenetically closer to Recent species than is *P. allinghamensis*. In most features it is more plesiomorphic than *P. nasuta* and *P. eremiana*; however, its relationships to *P. bougainville* and *P. gunnii* are unresolved. Considering its close phenetic similarity to *P. eremiana,* it may be the sister species to a *P. eremiana* — *P. nasuta* clade. Alternatively, it may lie outside of all Recent species of *Perameles* as their sister-species.

ACKNOWLEDGEMENTS

The Big Sink material was collected by M. Archer, A. Osborne and L. Dawson in October 1982. Phosphate Mine material from Wellington Caves was collected by A. Osborne and L. Dawson in May 1983. We are grateful of useful comments and advice provided by Ken Aplin and referees, and the assistance of Henk Godthelp, Mike Augee (University of New South Wales), Linda Gibson, Robert Jones (The Australian Museum) and the Wellington and Bow Shire Councils for permission to collect.

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